



## Description of *Bathynema nodinauti* gen. n., sp. n. and four new *Trophomera* species (Nematoda: Benthimermithidae) from the Clarion-Clipperton Fracture Zone (Eastern Tropic Pacific), supplemented with the keys to genera and species\*

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### Abstract

Seven specimens of the family Benthimermithidae from the Clarion-Clipperton Fracture Zone (Eastern Tropic Pacific), from the depths 4,800–5,040 m, were examined. *Bathynema nodinauti* gen. et sp. n. is described. The new genus differs from other genera of Benthimermithidae by the presence of an inner pharyngeal lumen. Four new species of *Trophomera* are also described. Body length of female of *T. elegantis* sp. n. approximately 1.5 mm; body cylindrical, anterior and posterior ends in shape of rounded cone; cephalic setae 2.0–2.5 µm long; trophosome consisting of 1 row of cells; female reproductive system didelphic, amphidelphic, occupying approximately 1/6 of total body length; ovaries reflected; diameter of mature eggs 17 µm; males not found. Body length of female of *T. minutissima* sp. n. 0.9 mm; body cylindrical, with thickest body part at anterior half of body; anterior and posterior ends rounded; cephalic setae 1.5 µm long; trophosome consisting of 1 row of cells; female reproductive system didelphic, amphidelphic, occupying approximately 1/3 of total body length; ovaries reflected; size of mature eggs 24x23 µm; males not found. Body length of female of *T. pacifica* sp. n. 5.4 mm; body cylindrical, anterior end rounded; posterior end conical, with thick conical terminal spine 81 µm long, showing granular core; cephalic setae 2.5 µm long inserted in tiny pits; trophosome consisting of 1 row of cells; female reproductive system didelphic, amphidelphic, occupying approximately 2/3 of total body length; ovaries outstretched; size of mature eggs 34x20 µm; males not found. Body length of female of *T. senckenbergi* sp. n. 1.6 mm; body fusiform; anterior and posterior ends in shape of a cone with rounded tip; cephalic setae 2 µm long; trophosome consisting of 1 row of cells; female reproductive system didelphic, amphidelphic, occupying approximately 1/6 of total body length; ovaries non-reflected; males not found. The new finding of *T. marionensis* is recorded. One rest specimen (in bad condition) of a new species is described as a morphotype. A dichotomous key to the genera of the Benthimermithidae and tabular keys to *Trophomera* species are presented.

**Key words:** *Benthimermis*, biodiversity, deep sea, taxonomy, manganese nodule, oozy sediments, taxonomy

### Introduction

At present, there are a number of nematode species, which are known as internal parasites with marine invertebrates as the definitive hosts. Most of these nematodes belong to the family Benthimermithidae. Larval (morphologically unidentifiable) stages of benthimermithids infest body cavities or internal organs of various marine nematodes, polychaetes, priapulids, and crustaceans (Hope 1977; Rubtzov 1980; Petter 1980; Petter & Goubault 1985; Chesunov 1988a, 1997; Miljutin 2004). Late parasitic stages can occupy the whole body of their hosts and, evidently, can result in the death of the host. Before terminal moulting, benthimermithids exit their host to the external environment, where they do not feed but do reproduce (at least as it has been inferred from their vestigial mouth and pharynx, and their intestine lacking an internal lumen).

Benthimermithids are deep-sea nematodes, which to date have been very rarely found. The hosts of the majority of the described benthimermithids are still unknown. Most species descriptions are based on very few non-feeding, free-living, adult specimens, either males or females. Both sexes are known in only two nominal species *T. australis* (Petter, 1983) (Petter 1983b) and *T. petterae* (Miljutin, 2004). Some species descriptions have been based on a single specimen.

Thirty three species of benthimermithids have been described to date. They are widespread from the Arctic to Antarctic and throughout the Atlantic and the Indian Oceans, but so far only six of them have been found in the Pacific Ocean (Rubtzov & Platonova 1974; Bussau 1993; Miljutin 2006). However, new benthimermithids were found when examining deep-sea meiobenthic samples from the cruise NODINAUT (Clarion-Clipperton Fracture Zone, Eastern Tropic Pacific).

The seabed in the study area was characterized by abyssal hills from 100 to 300 m in height, which were spaced 5 to 10 km apart. Most of the area (about 90%) between such hills (and on the hill slopes) was covered by ferromanganese nodules, the size of which varied from 2 cm to 15+ cm in diameter. Sediments between nodules were very fine-grained (<2µm) silicate oozes (radiolarian and diatomaceous) (Khripounoff *et al.* 2006).

Of the 5,700 nematodes examined from the samples of this cruise, seven specimens of benthimermithids were found (0.12% of examined nematodes). Five new species and one new genus, as well as one specimen of a known species, are described in the current paper. One specimen, clearly representing a new species, is described as *Trophomera* sp. because it was in too poor a condition for description.

## Material and methods

The specimens of benthimermithids examined in this study were in the marine nematode collection of the German Centre for Marine Biodiversity Research (Abt. DZMB, Senckenberg am Meer Wilhelmshaven, Germany). Samples were obtained in the Clarion-Clipperton Fracture Zone (Eastern Tropic Pacific) with either the 8-tube-multicorer (tube diameter 100 mm), the USNEL box corer (0.5m x 0.5m), or using the "Nautil" submersible: RV "L'Atalante", voyage NODINAUT (May–June, 2004), organized by IFREMER (Brest, France).

Once collected, the samples were initially fixed with 4% formaldehyde, buffered in seawater. Later, under laboratory conditions, meiobenthic organisms were separated from sediments using Levasil®-kaolin medium, following three consecutive centrifugations (McIntyre & Warwick 1984) at 4000 rpm for 6 min and rinsed in 70% alcohol. Then nematodes were sorted out, processed into glycerin using Seinhorst's method of slow evaporation (Seinhorst 1959), and permanently mounted on glycerin-paraffin slides. All nematodes were measured and studied using a LEICA DMR interference microscope with the x1.5 and x2 magnifier equipped with a camera lucida.

All type specimens were deposited in the Musée National d'Histoire Naturelle, Paris (MNHN) collection.

Abbreviations:

a: ratio of 'body length / maximum body width';

amph.dist.: distance from anterior end to amphid;

c: ratio of 'body length / tail length';

c': ratio of 'tail length / anal body diameter';

c.b.d: corresponding body diameter;

L: total body length;

V: distance from anterior end to vulva / total body length', %;

## Taxonomy

### Benthimermitidae Petter, 1980

#### *Bathynema* gen. n.

#### *Trophomera* Rubtzov & Platonova, 1974

*Diagnosis:* Benthimermithidae. Body cylindrical. Cuticle possessing fine striation visible in light microscope. Mouth opening absent. Four mediolateral head sensilla being papilloid. Amphidial fovea non-spiral, amphidial aperture pore-like. Pharynx possessing axial, internal lumen along most of its length. Cardia absent. Intestine being a trophosome devoid of an internal lumen. Male reproductive system diorchic, with two outstretched testes arranged consecutively in tandem and connected by joint spermaduct, a *vas deferens*, and paired spicules without gubernaculum. Caudal glands absent.

*Etymology:* From “bathyal” (deep sea) and “nema” (=Nematoda).

*Generotype:* *Bathynema nodinauti* sp. n.

*Differential diagnosis:* *Bathynema* gen. n. differs from other genera of family Benthimermithidae, *Trophomera* Rubtzov & Platonova, 1974 and *Adenodelphis* Petter, 1983 (Petter 1983a) by the presence of an internal pharyngeal lumen. Males of *Bathynema* gen. n. possess clearly curved spicules whereas spicules are hardly curved in all known males of the *Trophomera* genus (males unknown in *Adenodelphis* genus).

### Key to Benthimermithidae genera

- 1 Pharynx possessing distinct axial internal lumen over most of its length..... *Bathynema* gen. n.
- Pharynx devoid of distinct internal lumen..... 2
- 2 In females, numerous multicellular glands associated with oviducts present..... *Adenodelphis* Petter, 1983
- In females, multicellular glands absent on oviducts..... *Trophomera* Rubtzov & Platonova, 1974  
[= *Benthimermis* Petter, 1980; = *Abos* Rubtzov, 1980 (last revision: Miljutin 2006)]

#### *Bathynema nodinauti* gen. n. sp. n.

Figs 1–2; Table 1

*Type material:* Holotype: one mature male, collection number MNHN-BN493.

*Type locality:* Polymetallic nodule area, 14°02.7'N, 130°07.73'W, 4950 m depth, 03.06.2004, multicorer #16, corer #4.

*Etymology:* In honor of NODINAUT research cruise.

*Description:* Male. Body cylindrical, with thickest body part at anterior half of body; anterior end rounded, posterior end cone-shaped with thick and short cylindrical terminal part approximately 1/4 of tail, length rounded at its tip. Cuticle 2 µm thick and showing transverse striation along whole body length. Four short submedian cephalic setae 4 µm long inserted in tiny pits. Flat cervical lateral alae present at level of anterior part of pharynx, beginning at approximately 2/5 distance from anterior end to amphid and about 0.5 c.b.d. wide at level of amphid. Each lateral ala anteriorly single-lobed (approximately 2/5 ala length) and posteriorly bilobed (approximately 3/5 ala length). Amphid located at beginning of bilobed part of alae and between the lobes i.e. at approximately 1.6 c.b.d. from anterior end. Amphidial aperture round, 3.5 µm in diameter; *canalis amphidialis* with thick cuticular walls at distal part but gradually becoming thinner towards proximal end of the amphidial canal. Single lateral cervical short setae 3.0–3.5 µm long present between both posterior lobes of each ala at nearly double distance from anterior end to amphidial aperture. Mouth opening reduced to indistinct intracuticular apical tube. Pharynx slightly enlarged towards its posterior end and bipartite i.e. consisting of a short atrophied anterior part (10–15% of total length of pharynx) devoid of muscle cells and inner lumen and visible as a cellular mass, and a long posterior muscular part provided with an axial

inner lumen and surrounded by longitudinal muscles; this inner lumen also irregular with wide and narrow parts, as well as meandering. Several large hyaline cells situated around posterior part of pharynx. Nerve ring located at level of middle of pharynx. Two large hyaline cells approximately 0.5 c.b.d. in diameter located at anterior part of midgut; each cell with a large single nucleus and a single nucleolus. Cardia absent. Midgut an oligocellular trophosome without visible internal lumen and obviously consisting of 1 row of large cells, except most anterior part consisting of several small trophosomal cells. All trophosomal cells containing large hyaline granules; borders between cells distinct. Male reproductive system diorchic, occupying approximately 2/3 of total body length and consisting of two outstretched testes (each about 450 µm long) arranged consecutively in tandem and connected by joint spermaduct (130 µm long), *vas deferens* (650 µm long), and two spicules. Spicules moderately bent, consisting of long, relatively optically dense *lamina* and a short, funnel-shaped, relatively hyaline, proximal part (*capitulum*). *Capitulum* ventrally bent and evidently representing a flexible structure (this supposition is based on the location of *capitulum* at different angles in different spicules). Four midventral short supplementary setae present anterior to cloacal opening. Caudal glands absent.

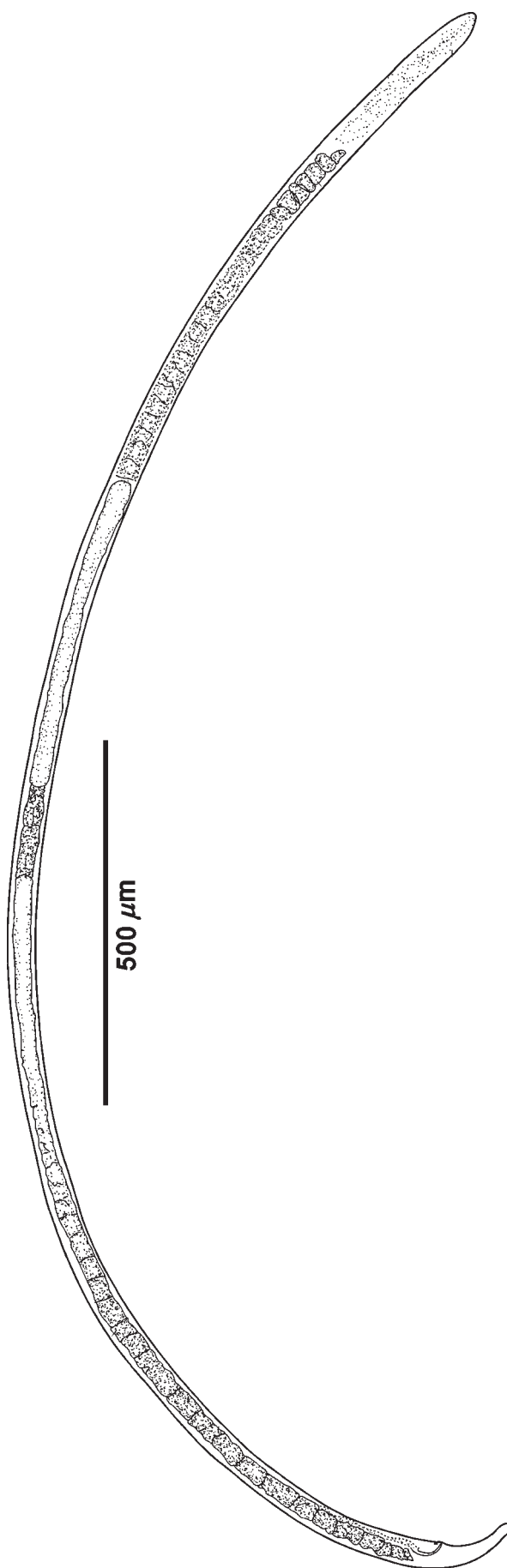
Host unknown.

Female, juvenile stages: unknown.

**TABLE 1.** Main measurements and characteristics of *Bathynema nodinauti* gen. n. sp. n., (male, holotype).

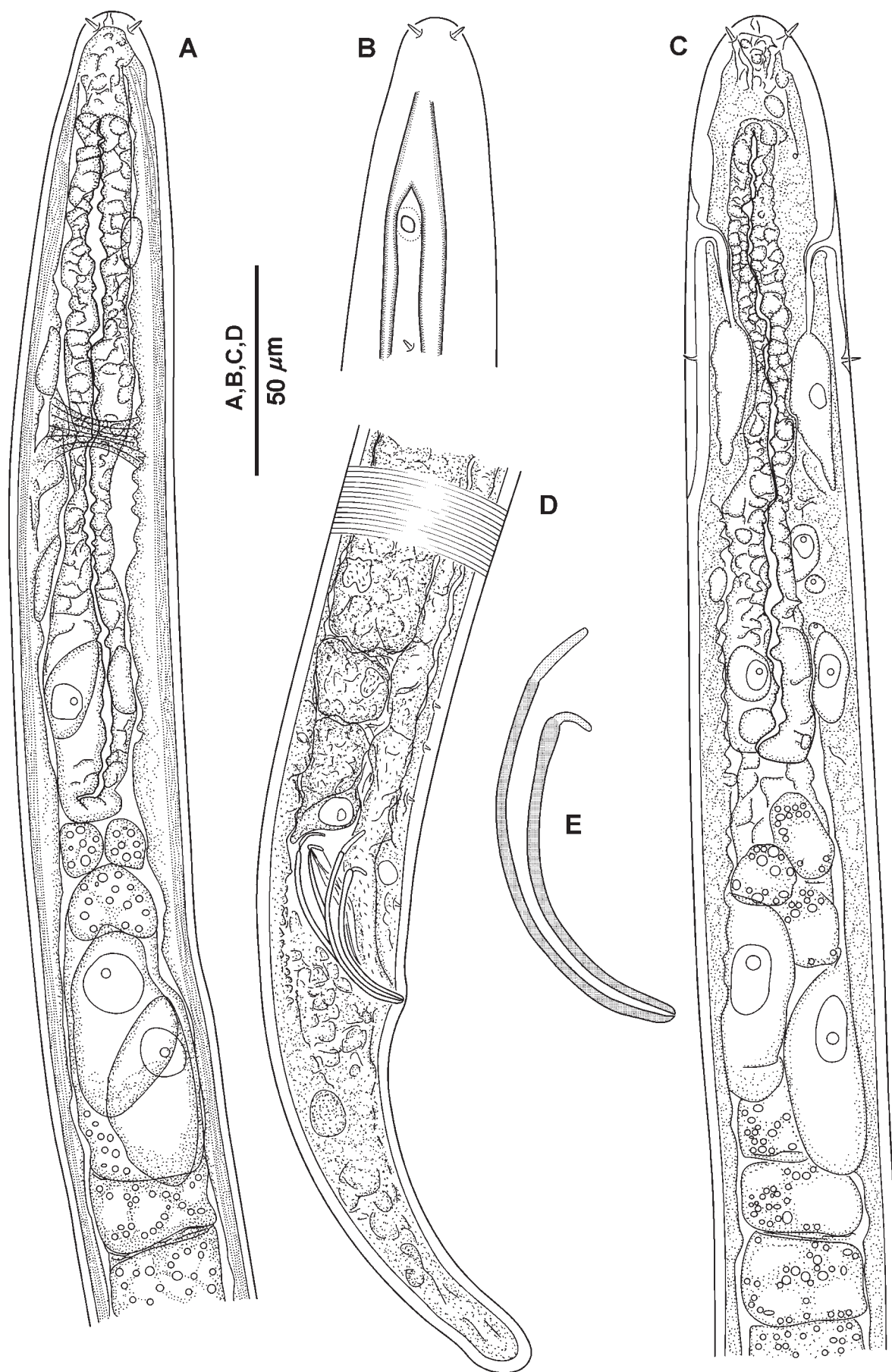
Degree of maturity	gravid
L, µm	2670
a	65.0
c	26.0
c'	3.2
Ratio of 'length of genital system / total body length', %	70
Amph.dist.	51
Cephalic sensilla length, mkm	4.0
Spicule length (µm):	
in chord	43
in arc	51
Amphidial aperture diameter, µm	3.5
Maximal body diameter, µm	45
Body diameter (µm) at level of:	
cephalic sensilla	16
amphid	36
1/4 body length	45
midbody	44
3/4 body length	42
anus	32

*Remarks:* Two large hyaline cells at level of anterior part of midgut may be considered as cellular bodies of secretory-excretory system (renetta). However, neither channel nor outlet of renetta has been found. However, these hyaline cells may be also interpreted as a vestigial dorsal gland. In earlier larvae of benthimermithids, this gland together with a stylet in the anterior part of pharynx forms a complex whereby larvae penetrate into host's internal issues (Chesunov 1997). This complex usually disappears at later larval stages, however, some mass of hyaline cells located between the pharynx and trophosome was also noted in male of *T. australis* (Petter 1983b).



**FIGURE 1.** *Bathynema nodinauti* gen. n. sp. n., male, holotype, total view.





**FIGURE 2.** *Bathynema nodinauti* gen. n. sp. n., male, holotype. A, anterior end, lateral view; B, anterior end laterally, surface view; C, anterior end, frontal view; D, posterior end; E, spicula.

***Trophomera* Rubtzov & Platonova, 1974**

= *Benthimermis* Petter, 1980 n. syn., = *Abos* Rubtzov, 1980 (op. Chesunov 1997)

***Trophomera elegantis* sp. n.**

Fig. 3; Table 2

*Type material*: Holotype: one gravid female, collection number MNHN-BN494.

*Type locality*: 13°55.63'N, 130°12.20'W, 4900 m depth, 2–5 cm sediment layer, 28.05.2004, submersible “Nautilé”, station 1597-5 CL 06.

*Etymology*: From Latin *elegans/elegantis* as adj. (slender, well-proportioned).

*Description*: Female. Body cylindrical, with fine cuticular transversal striation visible using light microscope; anterior and posterior ends in shape of rounded cone. Cuticle thickness approximately 2 µm along whole body. Amphidial apertures pore-like, 2 µm in diameter, located at 1.3 c.b.d. from anterior end. Amphidial fovea 3.5–4.0 µm in diameter; visible under cuticle. There are four submedian, thick papillae-like, cephalic setae 2.0–2.5 µm long at half the c.b.d. of their insertion from anterior end. Two cervical papilloid sensilla 1 µm long visible laterally before and behind amphid. Mouth opening reduced to a thin apical channel in cuticle. Pharynx a non-muscular, cellular mass devoid of an internal lumen; thin, axial, tube-like structure approximately 10 µm long visible in anterior part of pharynx only. Cardia absent. Midgut, an oligocellular trophosome without internal lumen and consisting of 1 row of cells at most part of body length; borders between cells indistinct. Trophosomal cells filled with large hyaline granules; density of these granules decreasing from anterior and posterior ends towards mid-body region. Rectum vestigial, in shape of hardly distinguishable duct. Anus also vestigial, visible as a thin transverse line/bar in cuticle. Female reproductive system didelphic, amphidelphic, occupying approximately 1/6 of total body length. Ovaries reflected, both about 120 µm long; anterior one lying at right side of body, and posterior one at left side. Oviducts short, with thin walls. Uterus with several mature eggs 24x23 µm in size. Neither morphologically differentiated spermatheca nor spermatozoa observed. Hyaline ring representing a circular vaginal sphincter visible around vagina. Caudal glands absent.

Host unknown.

Male, juveniles: unknown.

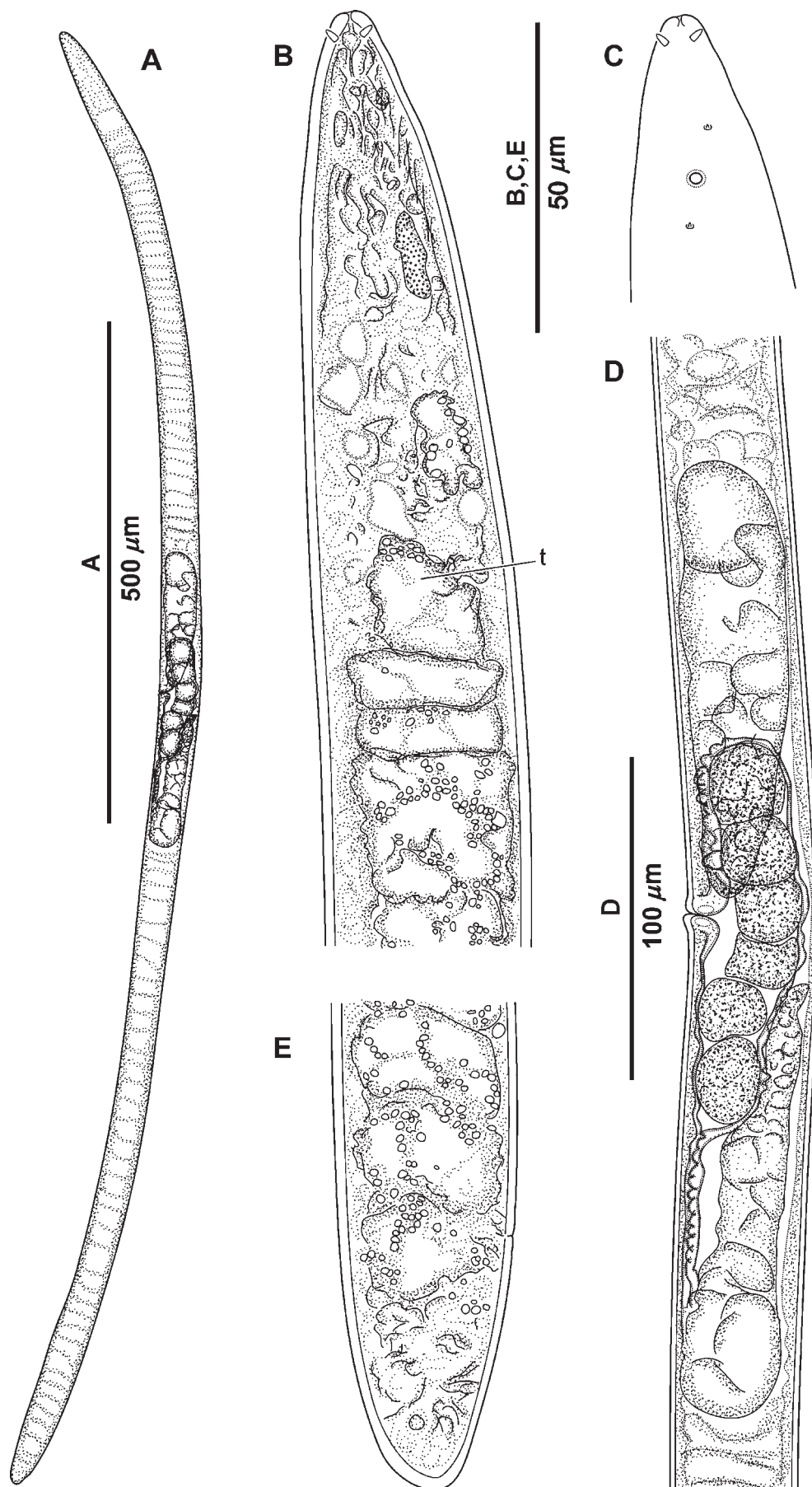
*Differential diagnosis*: *T. elegantis* sp. n. resembles *T. iturupiensis* Rubtzov & Platonova, 1974, *T. hureaui* (Petter, 1983) (Petter 1983b), and *T. conicauda* (Petter, 1987) by the shape and tail characteristics (tail in shape of rounded cone; ratio *c'* is 1.5; ratio “maximum c.b.d. / anal c.b.d.” is between 1 and 2).

The new species differs from *T. iturupiensis* by its shorter body length (1.5 mm vs. 26–38 mm), by the size of the cephalic sensilla (2.0–2.5 µm vs. 30–32 µm), by the structure of the trophosome (consisting of one row of cells vs. several cells on the sagittal optical section).

*T. elegantis* sp. n. differs from *T. hureaui* by its shorter body length (1.5 mm vs. 2.5–3.8 mm); by the smaller length of the mature, female genital system (occupying 1/6 body length vs. 1/4–1/3 body length); by the relatively bigger size of the eggs (ratio “c.b.d. at the uterus level / maximum egg diameter” = 1.8 vs. 4.0–5.0); by the caudal tip shape (rounded vs. pointed).

*T. elegantis* sp. n. differs from *T. conicauda* by its shorter body length (1.5 mm vs. 5.2–6.8 mm); by a thicker body (*a* = 37.3 vs. 49–58); by the relatively bigger size of the eggs (ratio “c.b.d. at the uterus level / maximum egg diameter” = 1.8 vs. 3.0). Each ovary of *T. elegantis* contains only 10–20 oocytes, whereas, in *T. conicauda*, number of oocytes in each ovary reaches hundred or more.

*T. elegantis* sp. n. resembles *T. minutissima* sp. n. by parameters of its female genital system (short reflected ovaries, short oviducts, few oocytes, and comparatively large mature eggs (ratio “c.b.d. at the uterus level / maximum egg diameter” is approximately 2 in both species). *T. elegantis* sp. n. differs from *T. minutissima* by its tail shape (in shape of rounded cone vs. rounded); and by its longer and thinner tail (*c* = 36.3 vs. 81.8 and the ratio “tail length / anal body diameter” = 1.5 vs. 0.55).



**FIGURE 3.** *Trophomera elegantis* sp. n., female, holotype. A, total view; B,C, cephalic end, lateral view; D, female genital system; E, posterior end. Abbreviation: t = trophosoma.



**TABLE 2.** Main measurements and characteristics of *Trophomera* species found in Clarion-Clipperton area. Key to symbols (L, a, c, c', V, and amph.dist.) is given in the list of abbreviations.

Measurements and characteristics	<i>T.elegantis</i> sp. n.	<i>T.marionensis</i> (Petter 1983b)	<i>T.minutissima</i> sp. n.	<i>T.pacifica</i> sp. n.	<i>T.senckenbergi</i> sp. n.	<i>T.sp.</i> <sup>a*</sup>
Sex	female	female	female	female	female	male
Degree of maturity	gravid	virgin	gravid	gravid	virgin	senile
L, µm	1490	10215	900	5430	1560	6615
a	36.3	60.1	27.3	44.5	22.6	92.0
c	36.3	60.6	81.8	45.6	44.6	101.8
c'	1.5	2.4	0.55	2.4	1.7	1.3
V (%)	45.0	57.3	54.4	51.6	46.2	? <sup>b**</sup>
Ratio of 'length of genital system / total body length', %	17	— <sup>c***</sup>	33	70	—	?
Amph.dist.	29	?	18	57	22	98
Cephalic sensilla length, µm	2.0–2.5	3.5	1.5	2.5	2.0	4.0
Spicule length (µm):						
in chord	—	—	—	—	—	49
in arc	—	—	—	—	—	49.5
Mature egg size (length x width), µm	24x23	—	17x17	34x20	—	—
Amphidial aperture diameter, µm	2.0	?	1.0	1.0	1.5	6.0
Maximal body diameter, µm	40	170	33	122	69	72
Body diameter (µm) at level of:						
cephalic sensilla	8	40	11	28	12	28
amphid	22	?	21	66	25	?
1/4 body length	33	167	33	122	69	?
midbody	41	170	30	115	75	72
3/4 body length	33	167	30	107	58	69
anus	28	70	20	50	19	51

a. \* Specimen in bad condition

b. \*\* It was impossible to measure this parameter.

c. \*\*\* Parameter is absent in this specimen.

### *Trophomera marionensis* (Petter, 1983)

Fig. 4; Table 2

Additional data and illustrations as *Benthimermis marionensis* in Petter (1983b): 9–10, Fig. 5; in Chesunov (1988b): 15–17, Figs 3–4; in Bussau (1993): 570–571, Fig. 247; and in Miljutin (2004): 32–34, Fig. 7.

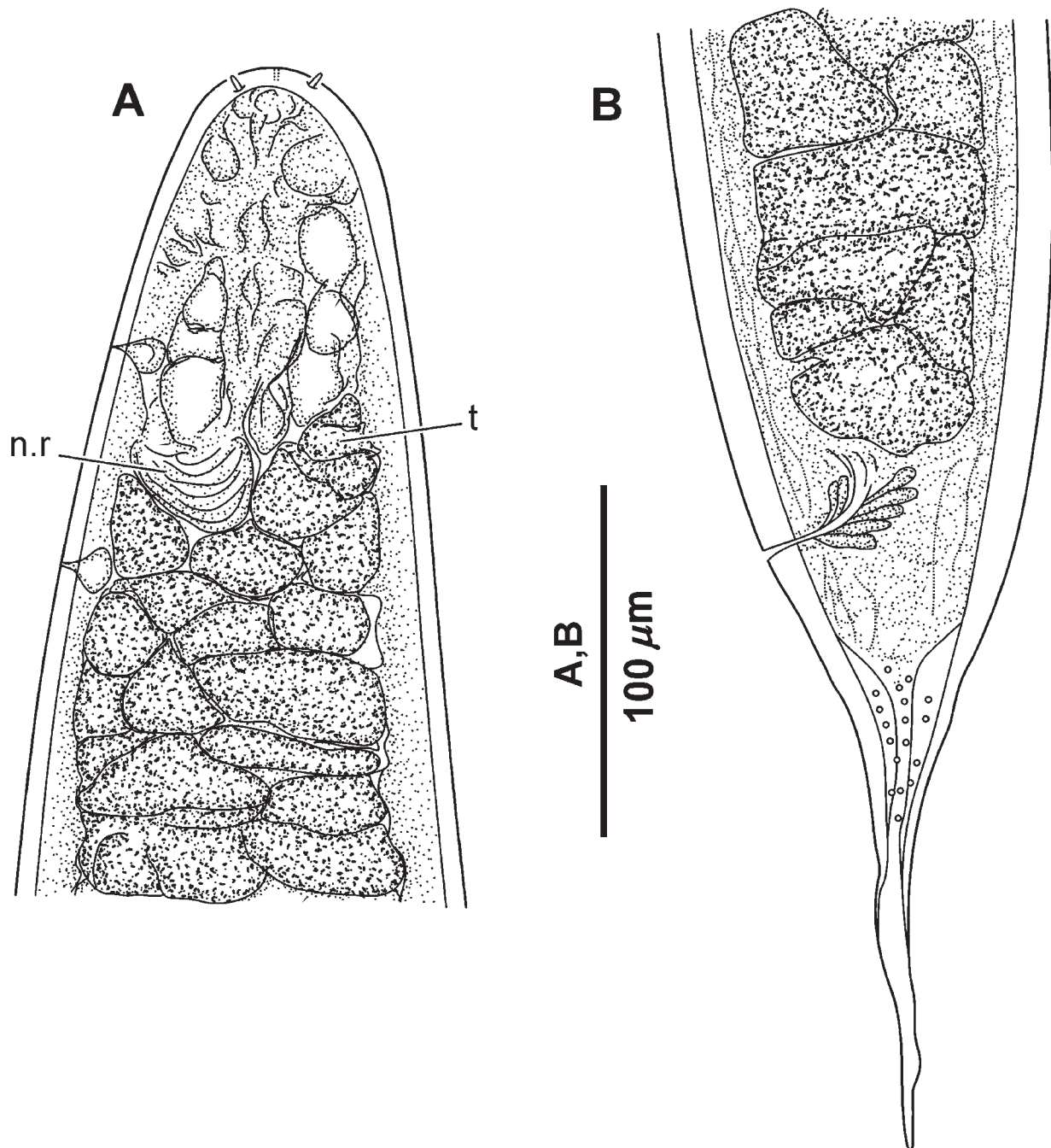
*Material*: One virgin female.

*Locality*: 13°55.63'N, 130°12.20'W, 4800 m depth, 2–5 cm sediment layer, 26.05.2004, submersible "Nautila", station 1595-3 CL 05.

*Description*: Female. Body thread-like, cylindrical. Anterior end in shape of a rounded cone. Posterior end conical, with a terminal spine 110 µm long, possessing a cytoplasmic core with granular inclusions. Mouth opening vestigial, looking like an obscure channel at apical part of head end. Four submedian papiloid cephalic setae approximately 3.5 µm long inserted in tiny pits. Amphids not observed. Pharynx a non-muscular, parenchymal string without an internal lumen. Nerve ring visible between pharynx and trophosome. Midgut, a multicellular trophosome without visible internal lumen, consisting of several rows of cells in optical section. Anterior trophosomal cells located ahead of posterior part of pharynx. Borders between trophosomal cells distinct. Rectum and anus present. Female reproductive system amphidelphic.

*Remarks*: *B. marionensis* was described upon eight gravid females from the southern part of the Indian Ocean, 46°52'S, 37°51'E, 31–110 m depth (Petter 1983b). Other specimens were described later by Chesunov

(1988b) from the Southern Atlantic (57°09'S, 26°09'W, depth 1729 m), by Bussau (1993) from the Eastern Pacific (07°04.04'S, 88°27.41'W, depth 4154 m), and by Miljutin (2004) from the Western Atlantic (8°07.88' N, 49°03.71' W, 4440 m depth). The new finding is the second record for the Pacific Ocean but it is far away from the previous region i.e. at a distance of about 5200 km. The new specimen agrees with the original description of *B. marionensis* in tail shape with terminal spine possessing a cytoplasmic core and structure of trophosome; body length and “V” value (10.2 mm and 57.3% vs. 9.3–14.8 mm and 46.5–74.0% respectively). However, the terminal spine of the new specimen is half as long as in the original description (110 µm vs. 200–320 µm) but closely resembles the specimen described in Miljutin (2004) (130 µm). Given the distance of the new specimen from the sites of the previous records, the slightly different morphological features may be attributed to differences between populations.



**FIGURE 4.** *Trophomera marionensis* (Petter 1983b), female. A, cephalic end; B, posterior end. Abbreviations: n.r = nerve ring; t = trophosome.

***Trophomera minutissima* sp. n.**

Fig. 5; Table 2

*Type material:* Holotype: one gravid female, collection number MNHN-BN495.

*Type locality:* 14°02.86'N, 130°05.35'W, 5040 m depth, 30.05.2004, multicorer #6, corer #2.

*Etymology:* From Latin *minutissima* (smallest).

*Description:* Female. Body cylindrical, with thickest body part at anterior half of body; anterior and posterior ends rounded. Transverse cuticular striation along whole body length hardly discernable using light microscope. Cuticle thickness 2.5 µm at anterior tip, 1.5 µm at mid-body region, and 3 µm at posterior tip. Amphidial apertures pore-like, 1 µm in diameter, located in 0.81 c.b.d. from anterior end. Amphidial fovea 3 µm in diameter visible under cuticle. Four submedian, setiform papillae 1.5 µm long. Mouth opening absent. Pharynx a non-muscular string devoid of an internal lumen. Cardia absent. Midgut, an oligocellular trophosome without visible internal lumen and obviously consisting of 1 row of cells. Numerous big, hyaline granules within trophosomal cells. Borders between trophosomal cells distinct. Anus and rectum present. Female reproductive system didelphic, amphidelphic, occupying approximately 1/3 body length. Ovaries reflected, 100–110 µm long, containing several tens of oocytes. Neither spermatheca, nor spermatozoa, nor vulvar glands observed. Hyaline ring representing a circular vaginal sphincter visible around vagina. Mature eggs in oviducts and uterus approximately 17 µm in diameter. Caudal glands absent.

Host unknown.

Male, juvenile stages unknown.

*Differential diagnosis:* The female of *Trophomera minutissima* sp. n. shows resemblance to females of *T. bathycola* (Rubtsov, 1980), *T. edouardensis* (Petter, 1983) (Petter 1983b), and *T. minuta* (Petter, 1987) by its reflected ovary and rounded tail without any process but differs from these species by its shorter body (0.9 mm vs. 2.3, 4.1, and 9.4 mm respectively). It is the smallest species in the genus *Trophomera*.

***Trophomera pacifica* sp. n.**

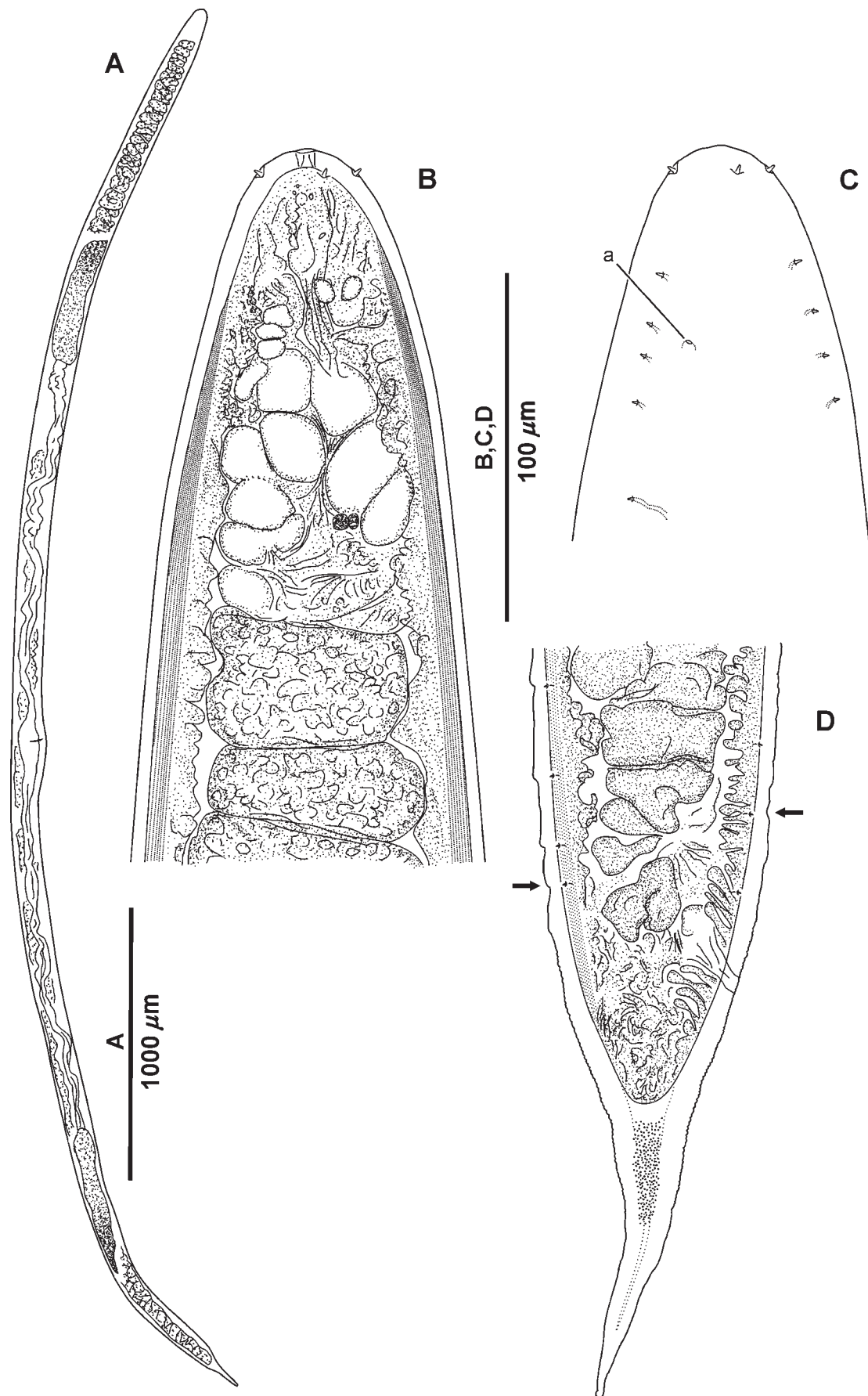
Figs 6–7; Table 2

*Type material:* Holotype: one gravid female, collection number MNHN-BN496.

*Type locality:* Polymetallic nodule area, 14°02.52'N, 130°07.98'W, 4950 m depth, 07.06.2004, multicorer #18, corer #2.

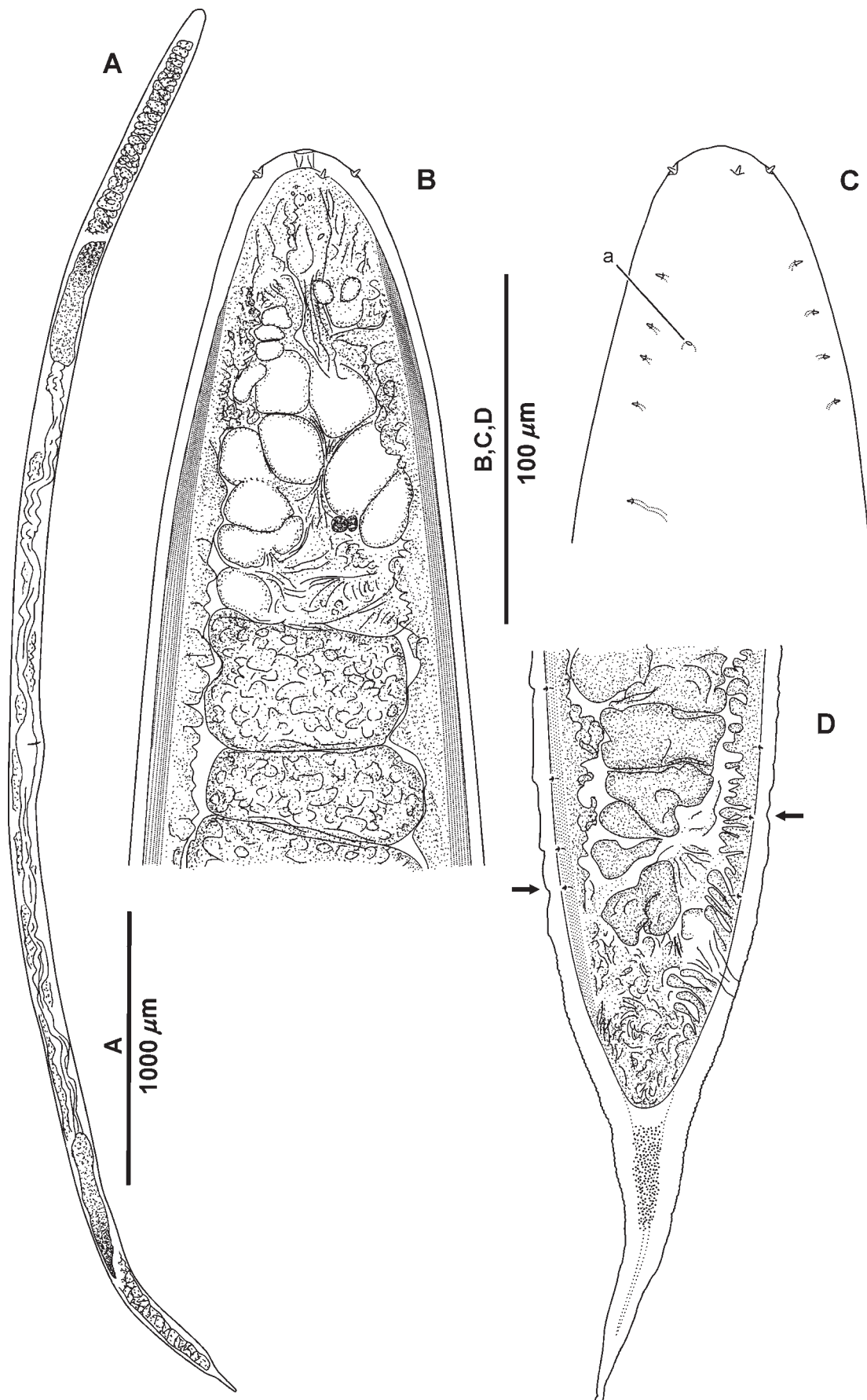
*Etymology:* “*Pacifica*” means “from the Pacific Ocean”.

*Description:* Female. Body cylindrical, with thickest body part at anterior half of body. Anterior end rounded, posterior end conical, with thick conical terminal spine 81 µm long, showing granular core. Cuticle with very thin and hardly visible transverse striations along whole body length; striations being more pronounced at caudal region. Cuticle thickness 5.5 µm at anterior tip, 4 µm at level of amphids, and 3 µm in the rest of the body parts. Amphids located at 0.86 c.b.d. from anterior end; amphidial apertures pore-like, 1 µm in diameter. Four submedian cephalic setae 2.5 µm long inserted in tiny pits. Somatic sensilla in shape of small papillae 1–1.5 µm long arranged in 4 longitudinal lateromedian rows from postamphidial region to anal region. Mouth opening reduced to a thin channel in cuticle. Pharynx a non-muscular string devoid of an internal lumen. Several large hyaline cells situated at posterior pharynx. Cardia absent. Midgut an oligocellular trophosome without visible internal lumen and obviously consisting of 1 row of cells. Borders between trophosomal cells distinct. Rectum reduced to an indistinctly visible tube. Female reproductive system didelphic, amphidelphic, occupying approximately 2/3 body length in the gravid specimen. Ovaries outstretched, 530 µm long in anterior branch, 715 µm in posterior branch. Oviducts very short. Uterus very long, occupying approximately 3/5 body length. Mature eggs 34x20 µm in diameter situated in one row in uterus except vulva region. Neither morphologically differentiated spermatheca nor spermatozoa observed. Vulvar glands present. Caudal glands absent.



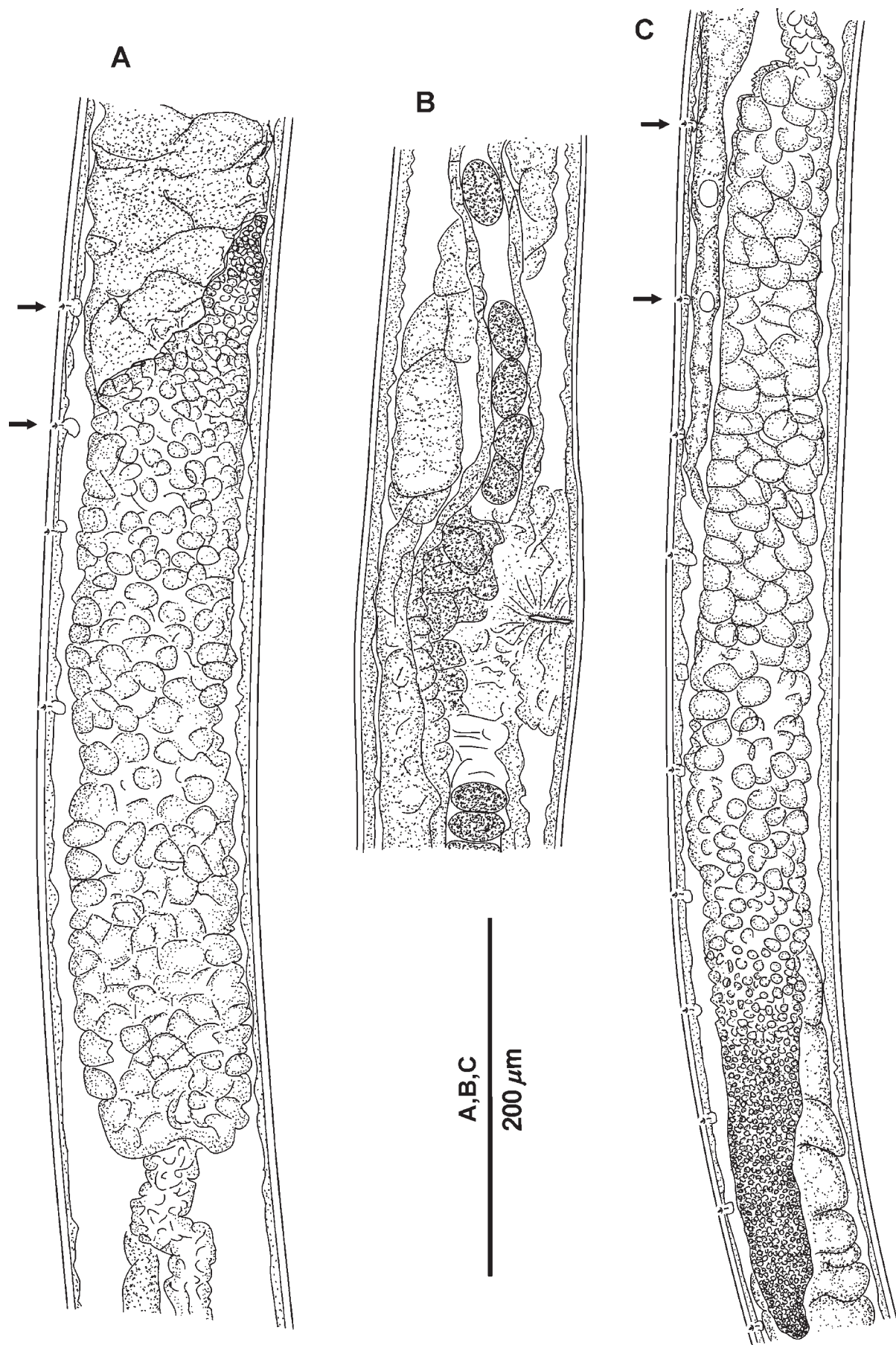
**FIGURE 5.** *Trophomera minutissima* sp. n., female, holotype. A, total view; B, genital system; C, cephalic end, lateral view; D, posterior end. Abbreviation: a = amphid.





**FIGURE 6.** *Trophomera pacifica* sp. n., female, holotype. A, total view; B, cephalic end, lateral view; C, anterior part of cephalic end laterally, surface view; D, posterior end (some small, hardly visible lateromedian, somatic sensilla pointed to by arrows). Abbreviation: a = amphidial aperture.





**FIGURE 7.** *Trophomera pacifica* sp. n., female, holotype. A, anterior ovary; B, vulva region; C, posterior ovary. Some small, hardly visible lateromedian, somatic sensilla are pointed to by arrows.

Host unknown.

Male, juvenile stages unknown.

*Differential diagnosis:* The female of *T. pacifica* sp. n. possesses outstretched ovaries. Only three *Trophomera* species have outstretched ovaries: *T. laubieri* (Petter 1987), *T. pseudominuta* (Miljutin 2004), and, possibly, *T. senckenbergi* sp. n.

*T. pacifica* sp. n. differs from *T. pseudominuta* by its larger body length (5.4 mm vs. 2.8 mm), and its tail shape (long conical spine vs. rounded).

*T. pacifica* sp. n. differs from *T. senckenbergi* sp. n. by its larger body length (5.4 mm vs. 1.5 mm), and its tail shape (long conical spine vs. cone-shaped with rounded tip).

In its general appearance, *T. pacifica* sp. n. strongly resembles *T. laubieri*. It differs from *T. laubieri* by: presence of a granular core inside the caudal terminal spine; a thickened cuticle at the cephalic apex; a difference in the ratio “distance from anterior end to amphid / c.b.d.” (0.86 vs. 0.72); trophosome structure (one row of cells at the longitudinal optical section vs. several rows); a longer female reproductive system (occupying approximately 0.7 body length vs. 0.45–0.50); egg size (34x20 µm vs. from 38x38 to 40x40 µm); and a different egg layout inside oviduct (only one row of eggs vs. several ones).

### ***Trophomera senckenbergi* sp. n.**

Fig. 8; Table 2

*Type material:* Holotype: one virgin female, collection number MNHN-BN497.

*Type locality:* 14°02.55'N, 130°05.35'W, 5035 m depth, 31.05.2004, multicorer #8, corer #2.

*Etymology:* In honour of Senckenberg Research Institute (Germany).

*Description:* Female known only. Body slightly fusiform, with thickest body part at first half of body. Anterior and posterior ends in shape of a cone with rounded tip. Cuticular, very thin, transverse, striation along whole body length being hardly visible except at caudal region. Cuticle thickness 1.5 µm at anterior tip and approximately 1 µm in rest body parts. Amphids located at 0.88 c.b.d. from anterior end; amphidial apertures pore-like, 1.5 µm in diameter. Four submedian, papilloid, cephalic setae 2 µm long inserted in tiny pits. Mouth opening reduced to a narrow, apical channel in cuticle. Pharynx looking like a non-muscular string devoid of an internal lumen. Cardia absent. Midgut an oligocellular trophosome without visible internal lumen and consisting of one row of big cells in longitudinal optical section. Borders between trophosomal cells distinct. Anus and rectum present. Female reproductive system didelphic, amphidelphic. Ovaries outstretched or hologonic (non-reflected) in single virgin specimen. No spermathecae nor sperm observed. Hyaline ring representing a circular vaginal sphincter visible around vagina. Caudal glands absent.

Host unknown.

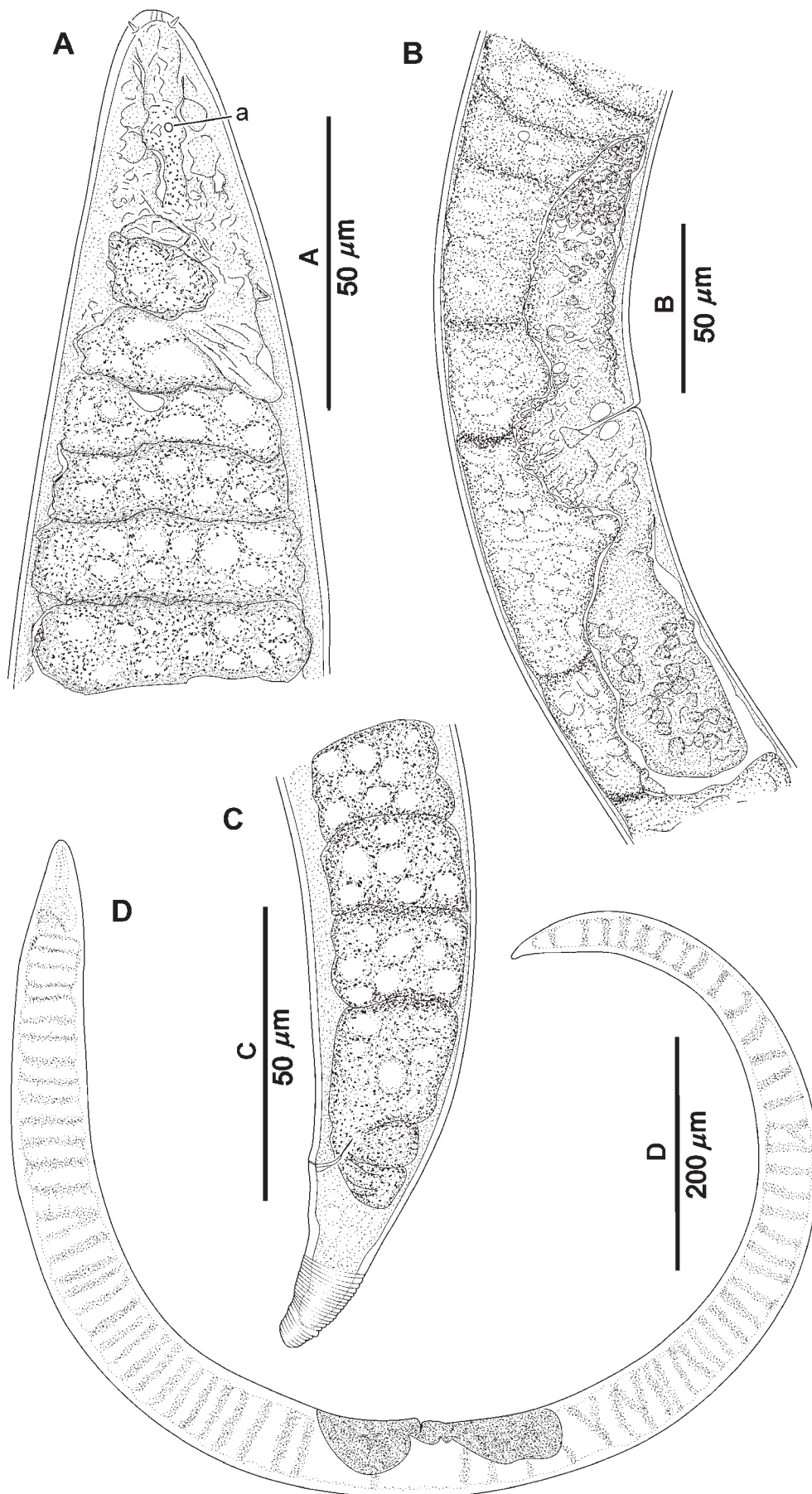
Males, juvenile stages unknown.

*Differential diagnosis:* The female of *Trophomera senckenbergi* sp. n. is characterized by a non-reflected ovary (it is impossible to clarify the certain construction because of immaturity of the type specimen). There are only five described *Trophomera* species, which have non-reflected ovaries: *T. megala* (Petter, 1987) and *T. turpicauda* Miljutin, 2004 possessing hologonic ovaries, as well as *T. laubieri* (Petter, 1987), *T. pacifica* sp. n. and *T. pseudominuta* Miljutin, 2004 possessing telogonic outstretched ovaries.

*T. senckenbergi* sp. n. differs from *T. megala* by its shorter body length (1.5 mm vs. 65–170 mm), body shape (fusiform vs. cylindrical), design of trophosome (oligocellular vs. multicellular), and its tail shape (conical with rounded tip vs. rounded with long terminal spine).

*T. senckenbergi* sp. n. differs from *T. turpicauda* by its shorter body length (1.5 mm vs. 3.4–6.1 mm), the body shape (fusiform vs. cylindrical), and its tail shape (conical with rounded tip vs. rounded with terminal, cuticular process of irregular shape).

*T. senckenbergi* sp. n. differs from *T. laubieri* and *T. pacifica* by its shorter body length (1.5 mm vs. 5.2–6.4 mm), the body shape (fusiform vs. cylindrical), and its tail shape (conical with rounded tip vs. conical with an edged elongated tip).



**FIGURE 8.** *Trophomera senckenbergi* sp. n., female, holotype. A, cephalic end, lateral view; B, primordial genital system; C, posterior end; D, total view. Abbreviation: a = amphid.

*T. senckenbergi* sp. n. differs from *T. pseudominuta* by its shorter body length (1.5 mm vs. 2.8 mm), its longer tail ( $c = 44.6$  vs. 86.9), and its tail shape (conical with rounded tip vs. rounded).

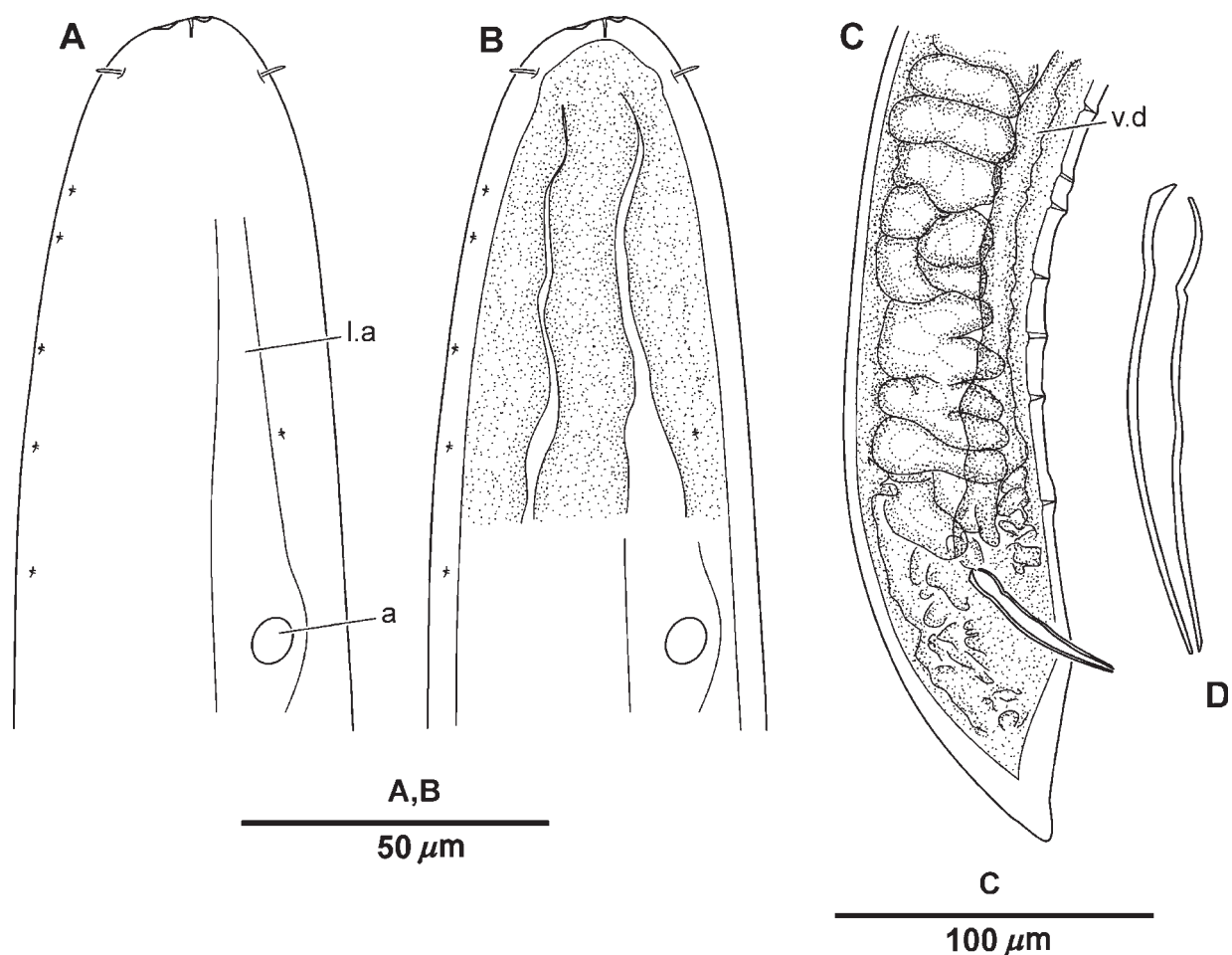
**Remarks:** The ovary of *T. senckenbergi* sp.n. is probably non-reflected. The reflected structure of ovaries is usually clearly visible even in virgin specimens (e.g. in *T. tchesunovi* (Miljutin, 2004) or in *T. petterae* (Miljutin, 2004)), whereas the structure of ovaries of virgin female of *T. turpicauda* (possessing a hologonic ovaries) was clearly non-reflected.

***Trophomera* sp.**

Fig. 9; Table 2

**Material:** One male in a bad condition though with most diagnostic features discernable.

**Locality:** 13°55.63'N, 130°12.20'W, 4900 m depth, 2–5 cm sediment layer, 28.05.2004, submersible “Nautilé”, station 1597-5 CL 06.



**FIGURE 9.** *Trophomera* sp., male. A, B, cephalic end; C, posterior end; D, spicula. Abbreviations: l.a = lateral ala; a = amphid; v.d = vas deferens.

**Description:** Body thread-like, cylindrical. Anterior end a slightly narrowing cone with rounded apex, posterior end a pointed cone shape. Transverse cuticular striation visible along whole body length. Cuticle thickness 3 μm along whole body length except terminal part of tail, where its thickness increasing to 6–10 μm, and 20 μm at caudal tip. Four submedian, short cephalic setae with rounded tips 4 μm long inserted in tiny pits. Two flat, cervical, lateral alae with a preamphidial part beginning at 1/3 distance from cephalic end to amphid and a postamphidial part (1/9 ala length). Amphidial aperture round, 6.0 μm in diameter. Short, somatic papillae approximately 1 μm long. Mouth opening reduced to a narrow apical tube. Pharynx a non-



muscular, cellular mass devoid of an internal lumen. Midgut an oligocellular trophosome without internal lumen and consisting of 1 row of cells. Borders between trophosomal cells distinct. Trophosomal cells consisting of large hyaline granules; density of these granules decreasing from anterior and posterior ends towards mid-body region. Spicules paired, almost straight. 15–16 mid-ventral, small, setiform supplementary organs present, from anterior to anus. Caudal glands absent.

Host unknown.

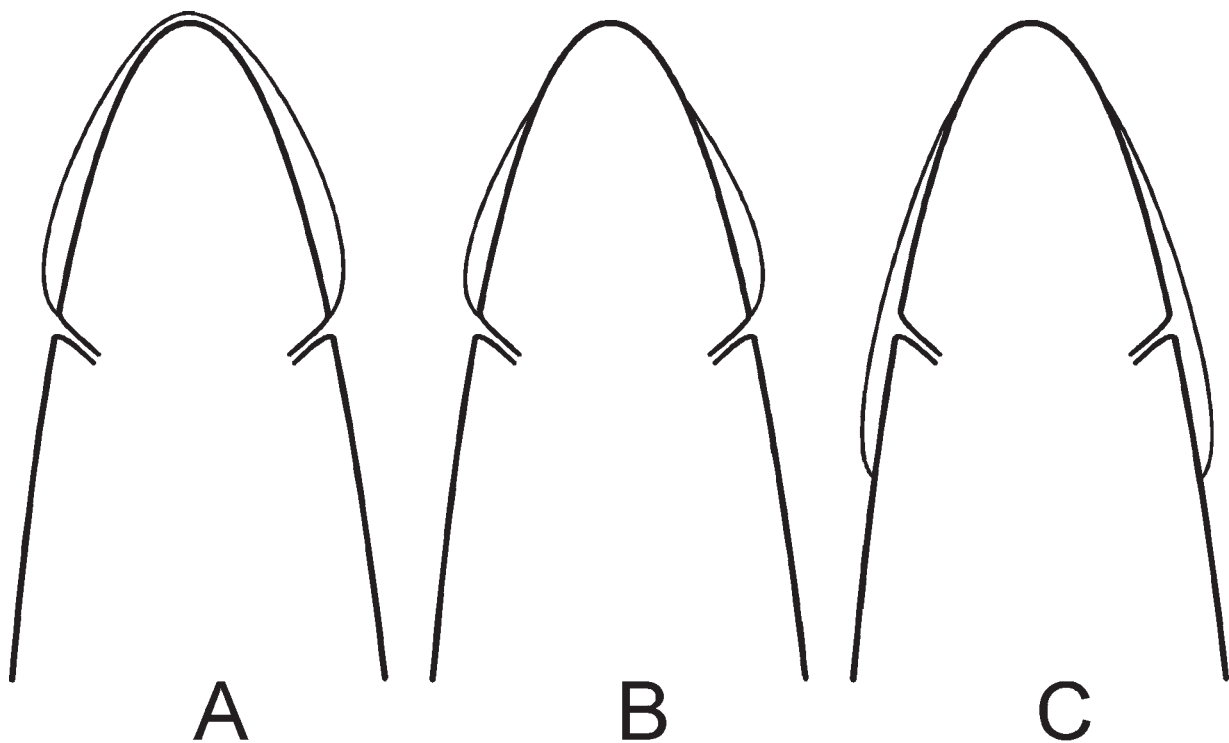
Females, juvenile stages unknown.

*Remarks:* The single specimen is in bad condition. Its body is strongly crumpled at the postamphidial part of the pharynx and beginning of the trophosome. The male reproductive system is wrinkled and collapsed, and it is impossible to ascertain its structure (number and arrangement of testes).

However, the described specimen evidently belongs to a new species of *Trophomera* because of its peculiar tail, characterized by a very thick cuticle. It only resembles *T. gracilis* (Petter 1982a) in the shape and structure of cervical lateral alae (long pre-amphidial part and short, not bilobed post-amphidial part). But, unlike the male specimen described, *T. gracilis* possesses a rounded tail. Unfortunately, the poor condition of the specimen does not facilitate good description and makes the specimen unsuitable for the status of holotype.

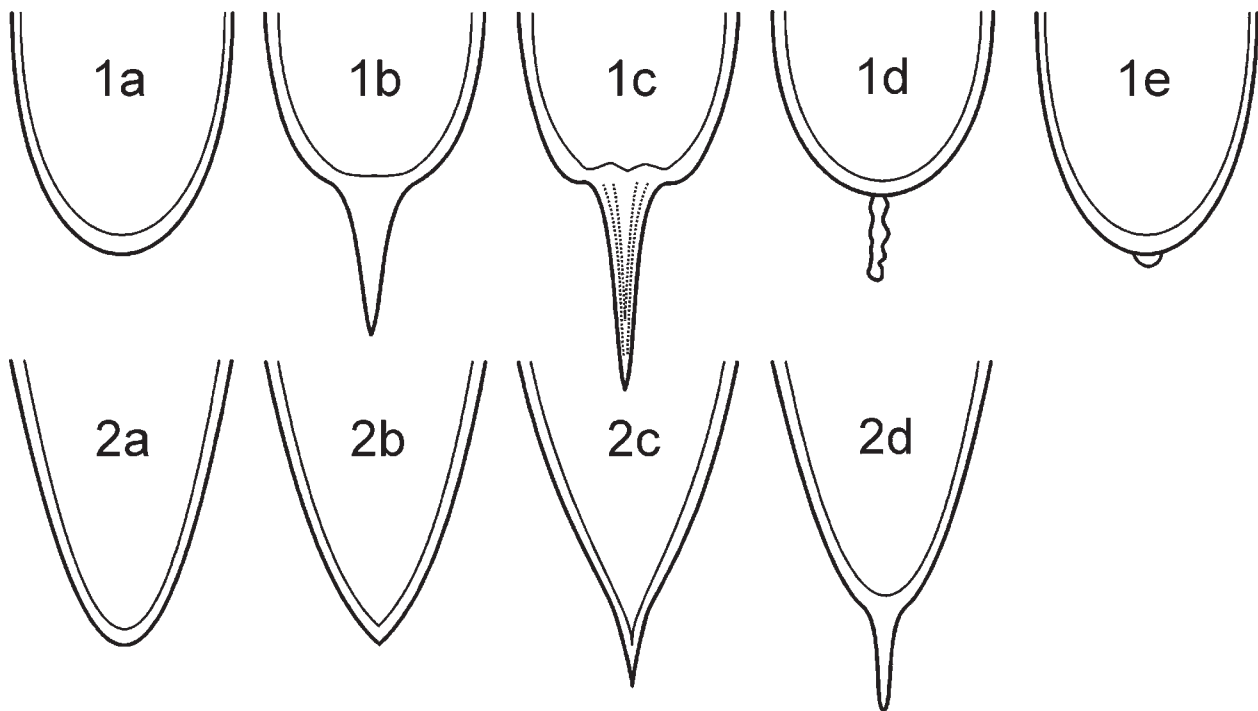
### Table keys to *Trophomera* species

The tabular keys to all known *Trophomera* species are presented in Tables 3 and 4. Because most of species were described on the basis of either males or female only, the keys for males and females are given separately. The keys are also supplemented with pictorial, schematic material on the main types of structure of male cervical lateral alae (Fig. 10), shape of tails (Fig. 11), and structure of male (Fig. 12) and female (Fig. 13) genital systems occurring in *Trophomera* species. These schemes should not be considered as morphological/phylogenetic series.



**FIGURE 10.** Main types of structure of cervical lateral alae occurring in males of *Trophomera* species. A, alae preamphidial, extending the whole distance from the cephalic apex to amphid; B, alae preamphidial, extending only a part of the distance from the cephalic apex to amphid; C, alae possessing preamphidial and postamphidial parts.





**FIGURE 11.** Main types of shapes of posterior ends occurring in *Trophomera* species. 1a, rounded tail; 1b, rounded tail with terminal spine; 1c, rounded tail with terminal spine possessing additional cuticular layers and granular inclusions; 1d, rounded tail with abnormal terminal spine; 1e, rounded tail with small terminal knob; 2a, tail in shape of rounded cone; 2b, cone-shaped tail; 2c, cone-shaped tail with attenuatous tip; 2d, cone-shaped tail with terminal spine.

## Discussion

The new findings of the pacific benthimermithids are from sites located far from previously known records in the Pacific Ocean. Bussau (1993) described 2 new species and 2 known species from the Atlantic and from the deep-sea area (DISCOL area, 07°04'S, 88°27'W, the Eastern Pacific) located at a distance of about 5200 km from the area of the new findings. Two species were described from the tidal zone on the Kuril Archipelago (North-western Pacific, about 7800 km from the area of the new findings) by Rubtzov and Platonova (1974) and Miljutin (2006).

So, at present, among 38 known species of benthimermithids, 11 species were described from the Pacific (in 4 publications), 9 species from the Indian Ocean (in 3 publications), and 32 species from the Atlantic (in 11 publications), both from northern and southern hemispheres. Several species were found in two oceans, and one species was described from three oceans.

It is obvious that benthimermithids are wide-spread in the World Oceans. It is highly likely the known, natural habitat of benthimermithids will be extended as new deep-sea areas of the world ocean will be studied.

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**TABLE 3.** A table key to the males of *Trophomera* species. Key to symbols (L, a, c, c', and amph.dist.) is given in the list of abbreviations.

Species name & authority	Structure of cervical alae*	Ratio "Length of preamphidial part of alae / amph.dist."	Ratio "Length of postamphidial " part of alae / amph.dist."	Ratio " L / cephalic sensilla, L, mm	a	c	c'	Shape of posterior end**	Structure of gonad***	Spicule length in arc, µm	Number of supplements		
<i>T.abysalis</i> (Bussau, 1993)	B	0.7	–***	67–72	5–6	5.9–7.2	66–72	54–70	1.5–1.9	2c,2d	C	70	16
<i>T.acuticauda</i> (Petter, 1981) (P. 1981a)	B	1.0	–	53–92	5	4.8–8.3	52	53–104	1.3	2c	C	45–70	12–19
<i>T.aptera</i> (Petter, 1982) (P. 1982b)	B	0.1	–	49	3–5	3.7	74	74	1.1	2c,2d	C	30.00	19
<i>T.australis</i> (Petter, 1983) (P. 1983b)	A	1.0	–	87–123	7	3.3–4.3	41–54	65–86	1.0	2a	C	52–55	18–24
<i>T.breviptera</i> (Petter, 1982) (P. 1982b)	B	0.2	–	27–33	3–4	3.5–5.1	102	58–73	1.3–1.4	2c	A	30–40	12
<i>T.crosetensis</i> (Petter, 1983) (P. 1983b)	B	0.7	–	68–82	5	4.0–4.5	40–45	31–32	2.0–2.1	2b,2c	C	50–60	14–22
<i>T.diploptera</i> (Petter, 1981) (P. 1981b)	C	0.3	0.7	53–115	3	6.6–15.0	130	83–300	1.3	2b,2c	E	70–120	18–68
<i>T.gracilis</i> (Petter, 1982) (P. 1982a)	C	0.7	0.3	53–76	4	4.4–6.1	72–98	285–543	0.5–0.6	1a	D	75–100	16–26
<i>T.improvisa</i> (Miljutin, 2004)	B	0.3	–	73	2.5–3	4.8	88	92	1.5	2a	F	28.00	9
<i>T.leptosoma</i> (Petter, 1981) (P. 1981a)	A	1.0	–	42–147	4	4.2–6.6	86	53–120	1.3	2b,2c	C	38–50	14–38
<i>T.litoralis</i> Miljutin, 2006	C	0.7	0.7	123–145	17	5.8–9.3	67–107	61–97	1.1–1.4	2a	C	50–76	>100
<i>T.petterae</i> (Miljutin, 2004)	B	0.7	–	68	5	5.8	78	70	1.6	2b,2c	B	29.00	10
<i>T.platyptera</i> (Miljutin, 2004)	A	1.0	–	69	1.5	3.0	84	102	0.8	1a	C	19.00	2
<i>T.regalis</i> (Bussau, 1993)	C	0.3	0.7	83	10	14.8	124	136	1.5	2b	C	130	49
<i>T.rosaliae</i> (Chesunov, 1988) (Ch. 1988b)	B	0.7	–	75	4–5	4.7	50	31	2.3	2c	C	55–58	11–15
<i>T.rotundicauda</i> (Petter, 1981) (P. 1981a)	A	1.0	–	83–98	6–7	10.0–13.8	94	321–630	0.3	1a	C	140–160	≤12

\* See Fig. 10.

\*\* See Fig. 11.

\*\*\* See Fig. 12.

\*\*\*\* Postamphidial part of alae is absent.

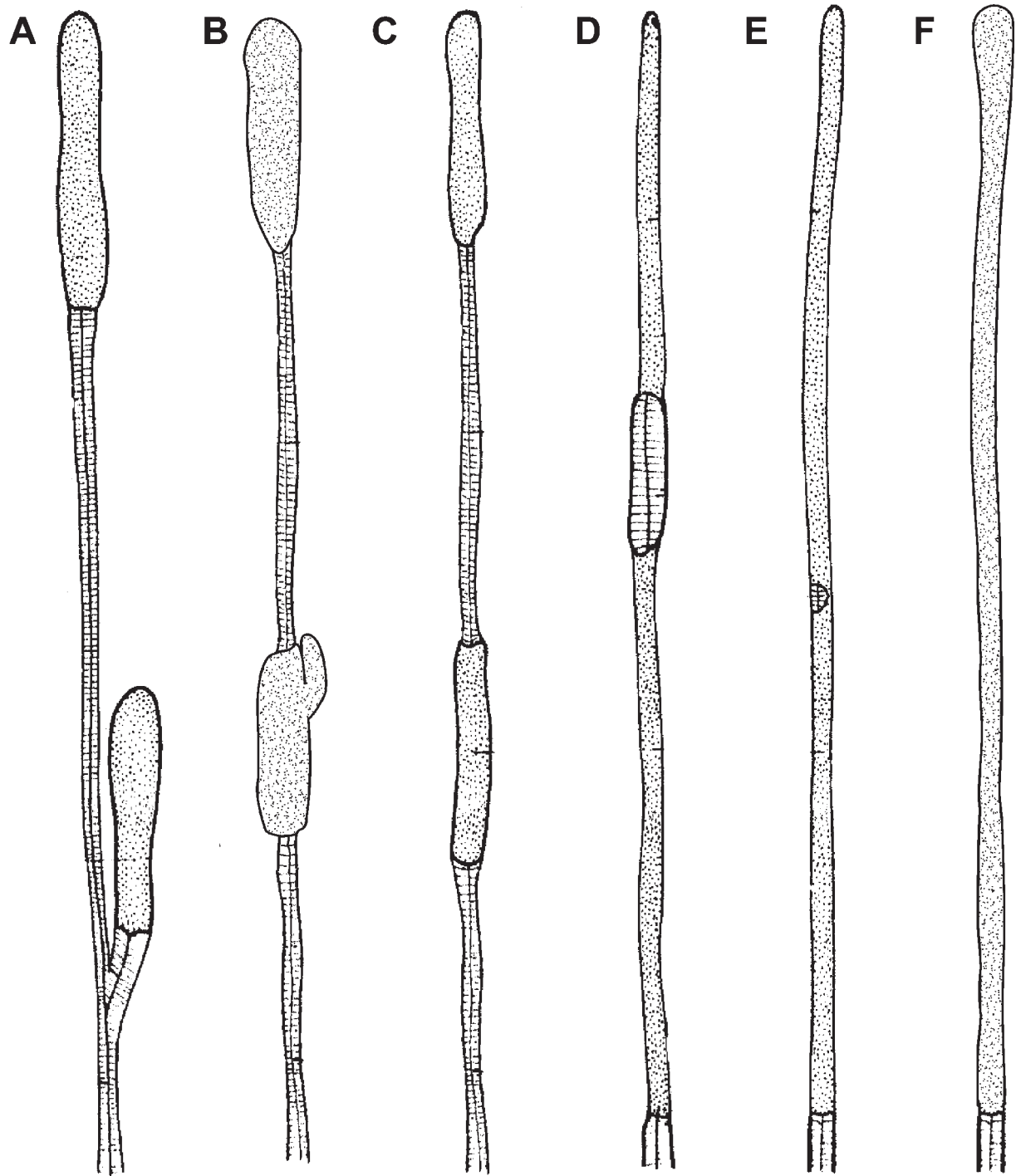
**TABLE 4.** A table key to the females of *Trophomera* species. Key to symbols (L, a, c, c', V, and amph.dist.) is given in the list of abbreviations.

Species name & authority	L, mm	a	c	c'	V	Length of cephalic sensilla,		Ratio “L amph.dist.”	Shape of posterior end*	Structure of female gonad**	Ratio “Total length of genital x system / L”	Maximum mature egg size (length x width), µm	Other references
						µm	µm						
<i>T.arnaudi</i> (Petter, 1983) (P. 1983b)	5.6–6.8	24–42	80–335	0.3	48–56	3–8	97–134	1a, 1e	A	A	0.5	30x20	Chesunov 1988b
<i>T.australis</i> (Petter, 1983) (P. 1983b)	4.4–9.4	25–38	67–104	7	50–60	6–7	133–152	2d	A	A	0.3	30x30	Chesunov 1988a
<i>T.baticola</i> (Rubtsov, 1980)	4.1	30	***	?	50	2–6	137	1e	B	B	?	20x20	Chesunov 1997
<i>T.conicauda</i> (Petter, 1987)	5.2–6.8	49–58	55–62	2.0	48–53	2	108–148	2a	A	A	0.25	30x25	
<i>T.edouardensis</i> (Petter, 1983) (P. 1983b)	8.6–9.4	27–29	8–312	0.4	48–55	4	156	1a	A	A	0.8–0.9	30x20	
<i>T.elegantis</i> sp. n.	1.5	36	36	1.5	45	2.0–2.5	51	2a	A	A	0.2	24x23	
<i>T.filiformis</i> (Petter, 1987)	3.7–5.5	39–59	36–74	1.4–2.4	47–57	1–2	33–97	2c, 2d	A	A	0.3	20x15	Miljutin 2004
<i>T.hopei</i> (Petter, 1980)	6.1	35	45	1.4	48	4–5	121	2c	A	A	0.25	60x40	
<i>T.hureai</i> (Petter, 1983) (P. 1983b)	2.5–3.8	25–32	42–62	1.1–1.2	48–56	3–4	71–94	2a, 2b	A	A	0.25	25x25	Miljutin 2004
<i>T.ifremeri</i> (Miljutin, 2004)	5.3	33	71	0.6	55	4	92	1a	A	A	0.2	?	
<i>T.iturupiensis</i> (Rubtsov & Platonova, 1974)	26.0–38.0	98–104	148	?	53–54	30–32	360–390	1a, 2a	?	?	?	?	Miljutin 2006
<i>T.laubieri</i> (Petter, 1987)	5.2–6.4	32–56	52–80	1.6–1.9	48–53	4	104–128	1b, 2c, 2d	B	B	0.5	40x40	
<i>T.marionensis</i> (Petter, 1983) (P. 1983b)	9.0–16.4	47–74	46–61	2.4	37–57	2–5	107–174	1c	A	A	0.2–0.3	?	Chesunov 1988b; Bussau 1993; Miljutin 2004; present work
<i>T.megala</i> (Petter, 1987)	65.0–170.0	103–174	?	?	41–54	7–9	260–622	1c	D	D	0.5	60x50	Miljutin & Tchesunov 2001
<i>T.minuta</i> (Petter, 1987)	2.3–2.8	18–20	88–163	0.3	54–64	2	51–52	1a	A	A	0.2–0.3	33x25	Bussau 1993
<i>T.minutissima</i> sp. n.	0.9	27	82	0.6	54	1.5	50	1a	A	A	0.3	17x17	
<i>T.pacifica</i> sp. n.	5.4	45	46	2.4	52	2.5	95	2d	B	B	0.7	34x20	
<i>T.petterae</i> (Miljutin, 2004)	4.4–5.2	46–53	70	?	51–53	3	120–192	2d	A	A	0.25	?	
<i>T.pseudominuta</i> (Miljutin, 2004)	2.8	23	87	0.6	66	3.5	26	1a	B	B	0.2	?	
<i>T.senckenbergi</i> sp. n.	1.6	23	45	1.7	46	2	71	2a	not A	?	?	?	
<i>T.tchesunovi</i> (Miljutin, 2004)	2.0	38	56	0.9	52.0	1	54	2b	A	A	0.3	15x9	
<i>T.turpicauda</i> (Miljutin, 2004)	3.4–6.1	27–43	71–73	0.7–0.9	48–49	4	33–60	1d	C	C	0.15	19x16	

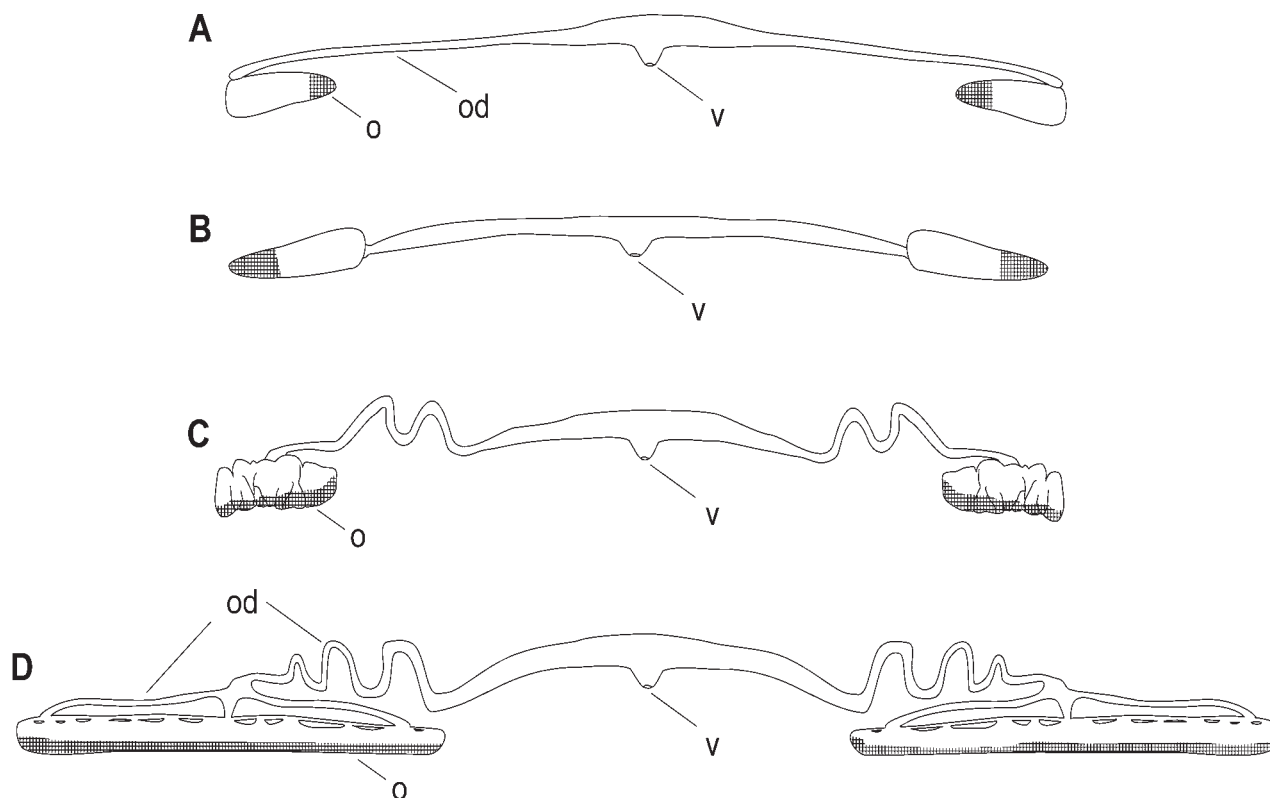
\* See Fig. 11.

\*\* See Fig. 13.

\*\*\* Not available for measure/observation or absent in the descriptions



**FIGURE 12.** Main types of *Trophomera* female reproductive systems. A, two testes directed anterior; B, testes arranged consecutively in tandem and connected by joint spermaduct, posterior testis having a small caecum directed anterior; C, testes arranged consecutively in tandem and connected by joint spermaduct; D, testes arranged consecutively in tandem and connected by joint shortened spermaduct; E, testes almost merged; F, testes merged in one long testis. From Miljutin (2004).



**FIGURE 13.** Main types of *Trophomera* female reproductive systems (germinal zones are indicated by the hatching). A, telogonic reflected ovaries (most species), B, telogonic outstretched ovaries (two known species); C, short hologonic ovaries; D, long hologonic ovaries. Abbreviations: o, oocytes or eggs; od, oviduct; v, vulva. From Miljutin (2004).

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